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THE EVOLUTION OF MAMMALIAN MOLARS TO AND FROM THE TRITUBERCULAR TYPE.[1]

BY HENRY FAIRFIELD OSBORN.

THE dentition in the recent Mammalia is so diverse that the most sanguine evolutionist of fifteen years ago could not have anticipated the discovery of a common type of molar, in both jaws, as universal among the Mmamalia of an early period as the pentadactyle foot, and as central in its capacity for development into the widely specialized recent types.

The tritubercular molar, discovered by Professor Cope in the Puerco, is exactly such a type, and may be considered with the pentadactyle foot as playing a somewhat analogous rôle in mammalian history, with this important difference—the unmodified pentadactyle foot was probably inherited direct from the reptiles, and its subsequent evolution, with a few exceptions, has been in the direction of the greater or less *reduction* of primitive elements towards special adaptation, as, to borrow an extreme illustration, in the transition from *Phenacodus* with 26 elements in the manus to *Equus* with only 12 such elements. On the other hand, the tritubercular tooth was not inherited, but in all probability developed within the mammalian stock, from a hypothetical form with almost, if not quite simple conical molars, implanted by single fangs, in a nearly homodont series.[2] No such primitive type of mammalian dentition is actually known, although *Dromotherium* approximates it; but the apparent reversion to this type among the *Cetacea*, and apparent retention of it in the *Edentata*,[3] support all the independent evidence upon this point derived from the Mesozoic Mammals. The principle of growth was the regular addition of new parts to the simple cone, not at random, but according to a certain definite order which apparently progressed independently in different phyla, through a series of sub-tritubercular stages until trituberculy[1] was attained.

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[1] Read in the geological section of the British Association at Bath, September, 1888. Read in abstract by Prof. Cope, National Academy is Sciences, at New Haven, Nov., 1888.

[2] See Author "Structure and Classification of the Mesozoic Mammalia." Jour. Phila. Academy, 1888, p. 240.

[3] See Oldfield Thomas, "The Homologies and Succession of the Teeth in the Dasyuridæ." Phil. Trans., 1887, p. 458.

The tritubercular molar consists essentially of three cusps, forming what may be called the primitive triangles, so disposed that the upper and lower molars alternate. This, when attained, formed a central stage from which the great majority of recent molar types have diverged by the addition, modification and reduction of cusps; we must except the Monotremes, the Edentates, and possibly the Cetaceans, although there is considerable evidence that the cetacean molars were once of the triconodont type.[2] Among extinct orders, the Multituberculata (*Plagiaulax*, *Tritylodon*, etc.) must also be excepted from this series and discussion.

The almost universal predominance of trituberculy in the early geological periods, is very significant of the uniformity of molar origin. Of twenty known Mesozoic genera,[3] all except three[4] show trituberculy in some of its stages. As to the Lower Eocene, eighty-two Puerco species, representing twenty-six genera and five orders (Creodonta, Tillodontia, Lemuroidea, Condylarthra, Amblypoda), only four species have quadritubercular teeth, all the remainder are tritubercular.[5] Prof. Rütimeyer has recently pointed out the predominance of this type in the nearly parallel Egerkingen beds The contemporary Cernaysien fauna in the collection of Dr. Lemoine at Rheims, recently examined by the writer, shows exclusively tritubercular molars or their derivatives. By the Middle Eocene the lines of divergence towards the existing types of molars were well advanced, but trituberculy persisted in the dentition of several orders, in which it is found to-day (Lemuroidea, Insectivora, Carnivora, and many Marsupialia).

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[1] First employed by Rütimeyer, "Ueber Einige Bezi ehungen zwischen den Säugethierstämmen Alter und Neuer Welt." Abh. d. schweiz. pal. gesellsch., Vol. XV., 1888, p. 54.

[2] See Brandt, "Die Fossilen u. Subfoss. Cetacean Europas." Taf. XXXII., figs. 4-9.

[3] The list given by the writer (op. cit., p. 247) is found to contain several synonyms. See "Additional observations upon the Structure and Classification of the Mesozoic Mammalia." Proc. Phila. Acad., Nov., 1888, p. 292

[4] Dicrocynodon (Diplocynodon), Docodon, Enneodon, Marsh.

[5] Cope, "Synopsis of the Vertebrate Fauna of the Puerco Series," Am. Phil. Soc., 1888. p. 298.

It follows that it is quite as essential for the comparative anatomist to thoroughly grasp the meaning and history of each of the component cusps of the trituberculer molar and of their derivatives, as it is to perfectly understand the elements of the manus and pes. For, the homologies of the cusps can now be determined almost as certainly as those of the digits. Take a human molar, for example, every component tubercle has its pedigree, and it can be demonstrated, almost beyond a doubt, which of these tubercles is homologous with the single reptilian cone. The writer recently (op. cit., p. 242) proposed the adoption of a distinct nomenclature for the different cusps of the tritubercular molar, and offered a series of terms for the primary cusps based as far as possible upon the primitive position and order of development, and in most instances in accord with their secondary position. This nomenclature can be extended to the secondary cusps in the sextubercular superior, and quinquetubercular inferior molars. The terms now in general use are based, for the most part, upon the secondary or acquired position, and in no instance upon the homologies of the cusps in the upper and lower molars, or even in corresponding molars of different genera, thus involving much confusion. For example, the Antero-internal cusp of the lower molar of *Mioclænus* is not homologous with the antero-internal cusp of *Hyopsodus*, nor with the antero-internal cusps of the upper molar of either genus.

The present contribution is based principally upon the writer's studies among the Mesozoic Mammalia, and, with some additions, upon Prof. Cope's numerous essays upon the tritubercular type in the Tertiary Mammalia.[1]

Four propositions may be laid down for discussion:—

(1.) That trituberculy was acquired during the Mesozoic period, in a series of stages beginning with the single cone and attaining to the primitive sectorial type in the Jurassic period.

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[1] Professor Cope's essays abound with discussions and notes upon the origin and succession of the tritubercular type. (See collection, in "Origin of the Fittest"). He has outlined the transition from the single cone to the tritubercular crown (p. 347); the tubercular sectorial (p. 246); the quadritubercular type (p. 245 and p. 359); the *Spalacotherium* molars as a transition to the *tritubercular* (p. 259). The acquisition of the superior and inferior quadritubercular molar (p. 361). The prediction of the discovery of Carnivora with triconodont molars (p. 365), and of the simple tritubercular type in both jaws (p. 362).

(2.) The majority of Mesozoic mammals showed trituberculy in some of its stages. Present evidence goes to show that the remaining, or aberrant types, if such existed, did not persist. The majority of the persisting forms of later periods were derived from the forms, with simple tritubercular molars, of earlier periods. It follows that trituberculy was an important factor in survival.

(3.) The definite homologies of the primary and to some degree of the secondary cusps in the upper and lower molars can be established.

(4.) The mode of succession of tooth forms favors the kinetogenesis theory advanced by Ryder and Coope.

There are three general observations to be made:—

First.—In attempting to complete the history of each of the cusps, we naturally find that the palæontological record is not sufficiently perfect to admit of our following a certain type along a single phylum back to the primitive type. We must at the outset proceed upon the principle of similar effects, similar causes. For example, since the history of the development of the intermediate tubercles in the superior molars of the Lemuroidea (Pseudolemuroidea, Schlosser) is perfectly clear during the Wasatch and Bridger epochs—it is safe to infer that the intermediate tubercles of the Ungulate molars, which are fully developed in the underlying Puerco, had the same history. *Second.*—There are in each period *Aberrant types* which embrace either incomplete or degenerate tritubercular stages, *i.e.*, a high specialization in which the past record is obliterated, or, finally, stages in non-tritubercular lines of development. *Third.*—In the parallel evolution of trituberculy in different phyla we find that the progression is by no means uniform. In every geological period in which the fauna is well known we observe *progressive* genera which outstrip the others in reaching a certain stage of molar development, contrasted with *persistent* types which represent arrested lower stages of development, while between them are the *central* types which represent the degree of evolution attained by the majority of genera. The latter may be said to constitute the stage which is characteristic of the period.

The Stages of trituberculy may now be defined as seen in different types in their order of succession:—

I. *Haplodont* Type (Cope).[1] A simple conical crown. The fang usually single and not distinguished from the crown. This type has not as yet been discovered among the primitive Mammalia.

A *Protodont* Tub. Type.[2] The crown with one main cone, and lateral accessory Cuspules; the fang grooved. There is some question as to the advantage of distinguishing this as a type, for it stands intermediate between types I. and III. Example, *Dromotherium* of the American Triassic.

II. *Triconodont* Type (Osborn, op. cit., p. 242). The crown elongate, trifid, with one central cone and two distinct lateral cones The fang double. Example, *Triconodon.*

III. *Tritubercular* (Cope)[3]. The crown triangular, surmounted by three main cusps, the central cone placed internally in the upper mollars and externally in the lower molars. Example, the lower molars of *Spalacotherium* and *Asthenodon.* This type is rare in its primitive condition as above defined.

> The upper and lower molars are alike in types I. and II.; in type III. they have a similar pattern but with the arrangement of the homologous cusps reversed. These types are all primitive. In the following sub types, the primitive triangle forms the main portion of the crown, to which other "secondary" cusps are added, the homologies of which in the upper and lower molars are somewhat doubtful. Parallel and with an intimate relation to the addition of the secondary cusps, is the division of the tritubercular into a secodont and bunodont series, according to the assumtion of a purely cutting or crushing function. In departing from the primitive type, the upper and lower molars diverge in structure, and the homologies of the secondary cusps in each are somewhat doubtful.

LOWER MOLARS.

A. *Tubercular Sectorial,* sub type (Cope). *a.* The primitive triangle elevated and its cusps connected by cutting crests; a low posterior heel. *b.* This type embraces a *quinquetubercular* form in which the heel consists of two cusps, an internal and external.[1] *c.* In the Bunodont series it develops into the *quadritubercular* form, by the loss of one of the primitive cusps.

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[1] "The Homologies and Origin of the Types of Molar Teeth in the Mammalia Educabilia." Journ. Phila. Acad., 1874. The term *Homodont* was previously applied to this type by Rütimeyer, "Odontographie der Hufthiere, etc." Verh. d. Naturforsch. Gesellsch. in Basel, Band. III., 1863, p. 563. In the writer's opinion this term has acquired a special significance as applied to a whole series of teeth, viz., the reverse of "heterodont," and may well be retained in this sense.

[2] Osborn, op. cit., p. 222.

UPPER MOLARS.

B. *Tritubercular.* *a.* The primitive triangle in the secodont series purely tricupsid. *b.* This embraces a *quinquetubercular* form in which "intermediate" tubercles are developed, both in the Secodont and Bunodont series. *c.* In the Bunodont series a postero-internal cusp is added, forming the *sextubercular* molar.

NOMENCLATURE OF THE CUSPS—As above stated, there is no doubt about the homologies of the three "primary" cusps (protocone, paracone, metacone) in the upper and lower molars They may be given the same terms, with the arbitrary suffix *id*, to distinguish the lower cusps. The first "secondary" cusps (hypocone-hypoconid), added to the upper and lower molars of the primitive triangle, modify the crown from a triangular to a quadrangular shape, and hence may be considered homologous. The three additional secondary cusps (protoconule, metaconule, entoconid) evidently have no homology with each other.

TERMS NOW IN USE.	PROPOSED TERMS.[2]	ABBREV.
Upper Molars.		
Antero-internal cusp	Protocone.	pr.
Postero- " " or 6th cusp	Hypocone.	h.
Antero-external "	Paracone.	p.
Postero- " "	Metacone.	m.
Anterior Intermediate cusp	Protoconule.	pl.
Posterior " "	Metaconule.	ml.
Lower Molars.		
Antero-external cusp	Protoconid.	pr.
Hostero- " "	Hypoconid.	h.
Antero-internal cusp, or 5th cusp	Parrconid.	p.
Intermediate or antero-internal cusp (in quadritubercular molars)	Metaconid.	m.
Postero-internal cusp	Eutoconid.	e.

Evolution of the Cusps. The cusp evolution in the Mesozoic period has been fully discussed by the writer (op. cit., pp.240-4)

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[1] American Naturalist, April, 1883, p. 407.

[2] I am much indebted to my colleagues Professors Macloskie and Winans for tie assistance in the selection of these terms.

PLATE XXV.

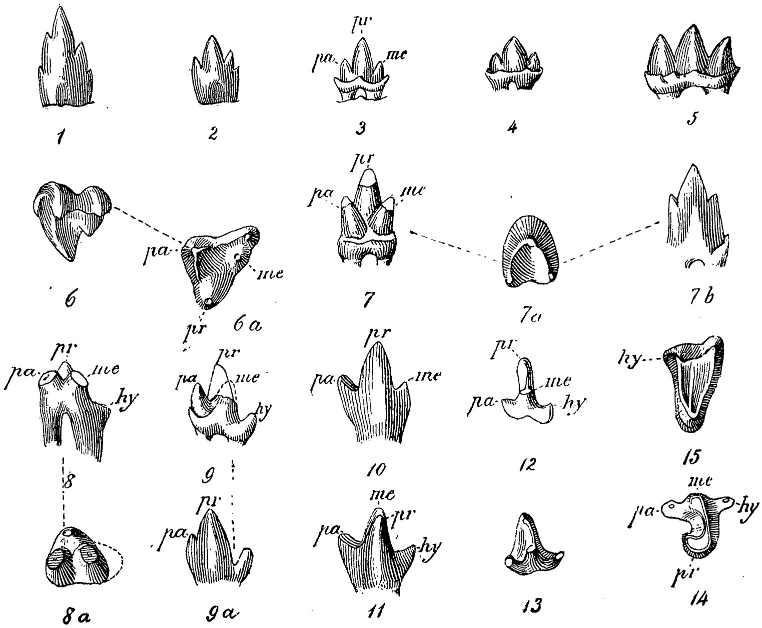

FIG. 1.

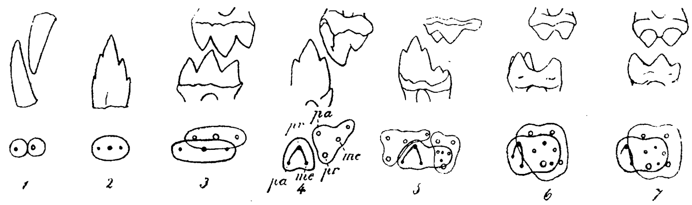

FIG. 2.

FIG. 1.—Molar teeth of Mesozoic Mammalia.
FIG. 2.—Molars of opposite jaws in normal mutual relation.

and in the Tertiary period, by Professor Cope, so that only a brief résumé is necessary here. In *Dromotherium* (fig. 1), from the upper Triassic, the oldest mammalian type known, with the exception of *Microlestes*, the molars have a main protoconid with several minute lateral cuspules, differing in size in the different teeth, but in general giving a trifid appearance to the crown. The molars of the contemporary *Microconodon* (fig. 2) also have unpaired fangs, but distinctly trifid crowns, with the anterior and the posterior cusps, or para and metaconids, upon the slopes of the protoconid. This Triconodont type reappears, with the addition of a cingulum and paired fangs, in *Amphilestes* (fig. 3) and *Phascolotherium* (fig. 4) of the lower Jurassic and persists in *Tricondon* (fig. 5) of the upper Jurassic. In this succession we observe especially the relative subsidence of the protoconid and upgrowth of the para- and metaconids. Contemporary with *Amphilestes* is the classical genus *Amphitherium* (fig. 6). A recent examination of the type specimen by the writer revealed the very interesting fact that the molars of this genus are probably of the primitive tubercular-sectorial types,—the oldest known example. Only the paracone and metaconids and hypoconids have been observed heretofore, but one can see the tip of the main external cusps between the former pair. This pattern is repeated, with a considerable elevation of the heel, in *Peramus* of the upper Jurassic.[1] Neither of the two foregoing are of the primitive heelless tritubercular type which is apparently found in *Spalacotherium* also upper Jurassic, and in the nearly related if not synonymous *Peralestes*, Plate XXV. Contemporary with the above, are numerous genera of the *Stylodon* order; among these, *Asthenodon* is of

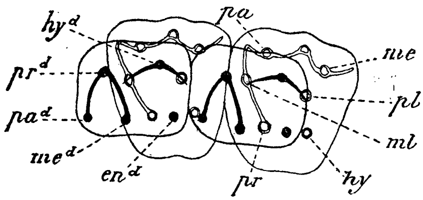

FIG. 1.—Diagram of quadritubercular molars of both jaws in normal mutual relation; the superior cusps double lines; the inferior black.

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[1] This genus includes also *Septocladus dubius* Owen, and *Spalacotherium minus* Owen. See Proc. Phila. Acad., Nov. 1888, p. 292.

the primitive tritubercular type without the hypoconid, all the remainder present various modifications of the tubercular sectorial·

This covers our knowledge of trituberculy in the Mesozoic period. No bnunodont forms are known—they were probably developed during the Cretaceous, for a few are found well developed in the Puerco. In the Sectorial series many of the types do not widely depart from those seen in the Jurassic, but the Bunodont series are universally characterized by the initial or advanced development of the proto- and metaconules in the upper molars and the apperance of the *Entoconid* upon the inner side of the hypoconid below.

The principles governing cusp development.—It is remarkable to note in how many particulars the actual succession of molar development in the Mesozoic period coincides with the theoretical scheme of origin of trituberculy proposed by Cope[1] and supported by Wortman[2] several years ago. At that time *Spalacotherium* and the genera now embraced under the *Triconodontidæ* were the only Mesozoic mammals whose molar structure was fully known, and the views of these authors were partly speculative and partly deductive from recent dental anatomy.

Two hypotheses may be advanced to explain the evolution of the ritubercular type. The first is that the type has been acquired by the selection of accidental variations in the production of new cusps and modelling of old ones. The second is, that the interaction of the upper and lower molars in the movements of the jaws has resulted in local increase of growth at certain points, resulting first in new cusps, then in a change of position and of form in the cusps. Both hypotheses are open to numerous objections and are by no means mutually exclusive, but the whole subject is so complicated as to require a separate treatment. The balance of evidence in tritubercular evolution seems to favor the second or kinetogenesis theory—as apparently witnessed in two laws of cusp development.

I. The primary cusps first appear as cuspules, or minute cones, at the first points of contact between the upper and lower molars in the vertical motions of the jaws.

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[1] "The Evolution of the Vertebrata Progressive and Retrogressive," American Naturalist, April, 1885, p. 350.

[2] "The Comparative Anatomy of the Teeth of the Vertebrata," 1886 p. 418.

II. The modelling of the cusps into new forms, and the acquisition of secondary position, is a concomitant of interference in the horizontal motions of the jaws.

The second law applies especially to the evolution of the molars after the acquisition of the tritubercular stage, and has been ably proposed and supported by Ryder,[1] principally in its application to recent types of teeth. The first, although not heretofore distinctly formulated, is partly founded upon facts and principles advanced by Cope, and applies chiefly to the stages which have been discussed in this essay.

During the Homodont mammalian or sub-mammalian molar stage, the jaws were probably isognathous and the simple cones alternated as in the *Delphinidœ* (fig. 1). The first additions to the protocone appeared upon its anterior and posterior surfaces. The growth of the para- and metaconids involved anisognathism,[2] for we find in the later triconodonts that the lower molars closed inside of the upper (*Triconodon*, fig. 2). There are several transition forms such as *Tinodon* and *Menacodon* between the primitive triconodont type and *Spalacotherium*, and it has been assumed by Cope and the writer (op. cit., p. 243) that the para- and metaconids were first formed upon the anterior and posterior slopes of the protoconid and then rotated inwards, but it is also possible that they were originally formed upon the inner slopes. In the complemental formation of the upper and lower triangles the jaws remained nearly isognathous (fig. 4). There is no evidence as to the origin of the hypoconid, which as a rule preceded the hypocone, as it was developed very early. In the *Stylacodontidœ*, *Phascolestes*, *Amblo-*

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[1] "On the Mechanical Genesis of Tooth Forms." Proc. Phila. Acad., 1878, p. 45.

[2] As employed by Ryder (op. cit., p. 45). "So as not only to indicate respectively parity and disparity in transverse diameter of the crowns of the upper and lower molars, but also the parity or disparity in width transversely, from outside to outside," etc.

It is clear that in the homodont condition, with the teeth simply piercing the food, the greatest comminution (of the food) is effected by isognathism; in the triconodont stage, the jaws must be anisognathous to close upon each other, but the tritubercular stage admits a return to isognathism by the alternation of the triangles.

therium, etc., the crowns rapidly increased in transverse diameter (fig. 7) and, in some genera, they (Kurtodon) so far lost the tritubercular aspect that, but for the connecting form *Asthenodon* (fig. 6), we might hesitate to place them in this series. The key to the further evolution of the crown is seen in the bunodont series during the lower Eocene period.

The superposition of the lower and upper molar patterns brings out many interesting facts. First, even in the complex crowns of the bunodont molars the primitive triangles retain their primitive alternating arrangement. Second, the jaws are somewhat anisognathous. Third, in support of the first law of cusp development, we observe that the protoconule and metaconule are developed at the points of contact with the ridges which extend from the hypoconid, and, secondly, that the hypocone appears at the point where the paraconid abuts against the protocone. It follows from a comparison of numerous species of *Pelycodus* and *Mioclœnus* that as the hypocone develops, the paraconid recedes, as first observed by Cope; a fact difficult to reconcile with the kinetogenesis theory. In this manner the inferior primitive triangle is broken, as the upper molars develop into the sextubercular and the lower into the quadritubercular type. The complemental development of the upper and lower molars in the known genera of successive horizons is approximately displayed in the subjoined table.

The Eocene list of genera will be greatly reduced, especially in the Tritub.-tuberc-.sectorial type, when the upper and lower jaws are found associated, and it must be clearly understood that the sub-types a, b, c, in the above table, are very closely related by transition forms. In fact, in the carnivorous forms, the extreme secodont and bunodont types are frequently seen side by side, as in the first and second inferior molars of *Didymictis*. The chief distinction between these two series is the greater development of the secondary cusps and the almost invariable loss of the paraconid in the latter; this is effected by the broader surfaces of contact in the bunodont crowns. In the secodont series, on the other hand, the development of the secondary cusps is subordinated, and the metaconid is almost invariably suppressed.[1]

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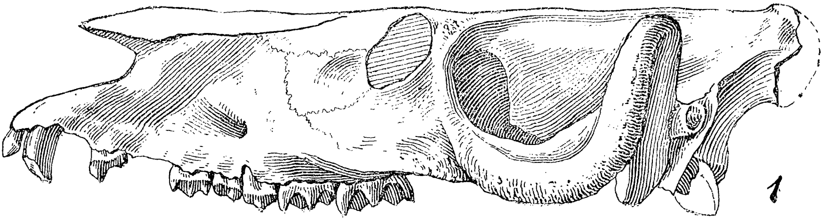
[1] See Cope: "Origin of the specialized Teeth of the Carnivora." Am. Naturalist, March, 1879.

PLATE XXVI.



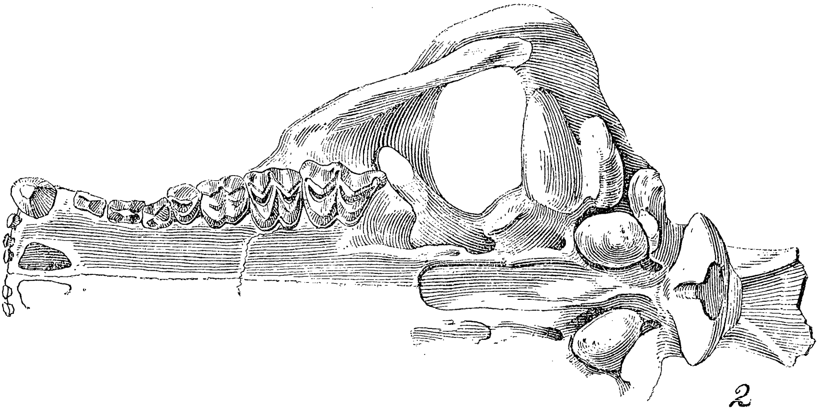


Fig. 1.—*Merycochœrus macrostegus* Cope. $\frac{1}{3}$
Fig. 2.—*Merycochœrus superbus* Leidy. $\frac{1}{3}$

	SECODONT SERIES.				BUNODONT SERIES.				
	I. A.	II.	III.	a.	a. c.	b.	c.		
Molars Upper......	....	Triconodont.	Tritubercular.	Tritubercular.	Tritubercular.	Quinquetuberc.	Sextubercular.	Aberrant.	Lophodont.
Molars Lower......	Protodont	Triconodont.	Tritubercular.	Tuberc. Sectorial.	Quadritubercular.	Quinquetuberc.	Quadritubercular.		Symborodont.
Middle Eocene,* Bridger..............	....	....	....	22	4	7	9	1	11
Lower Eocene,** Puerco..............	....	....	....	6	2	2	1	....	....
Upper Jurassic***..	....	3	2	5	....	....	....	4	....
Lower Jurassic......	....	3	....	1	....	....	....	....	....
Triassic..............	1	1	....	....	....	....	....	....	....

* From Prof. Marsh's list of Bridger genera, excluding the Rodentia (see various papers). The Insectivora and Creodonta belong to sub-type a; the Lemuroidea, to sub-types b and c.

** From Prof. Cope's list of Puerco genera (see "Synopsis, etc.").

*** From Author's list of Mesozoic genera (see op. cit., p. 247).

Adapis and *Anaptomorphus* are examples of Sub-types a, c, associated; for it frequently happens that the paraconid atrophies without a complete enlargement of the hypocone. A study of the diagram demonstrates, however, that the association of Sub-types b and c is impossible. The recent monkeys *Tarsius* and *Loris* afford a good illustration of the association of
tritubercular
quinquetubercular
sextubercular
and
quadritubercular
molars.

The subsequent evolution of the molars, in different orders, was characterized, first, by the loss of the primary cusps, *e.g.*, the metaconid in the Carnivora,[1] the paraconid in the Ungulata. Second, by the loss of some of the secondary cusps, *e.g.*, the proto- and metaconules in the Artiodactyla.[1] Third, by the metamorphosis in the form of the cusps. This subject has been fully treated by Rütimeyer, Kowalevsky, Cope, Schlosser and others.

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[1] Schlosser: "Beitrage zur Kenntniss der Stammgeschichte der Hufthiere," Morph. Jahrb., 1886, p. 123, has especially drawn attention to the probability that the Artiodactyla were derived from sexitubercular forms.

The Relation of Trituberculy to the Persistence of Mammalian Phyla.—The above table shows somewhat indefinitely, but none the less positively, the general progression of the Mammalia, to and from the primitive tritubercular type. As already stated, even with our present very limited knowledge, certain stages appear to have been characteristic of certain periods, as follows: the triconodont in the lower Jurassic; the primitive tritubercular and tubercular sectorial in the upper Jurassic; the secodont and bunodont subtypes of trituberculy, predominated in the Puerco; in the Bridger, the Perissodactyl ungulates had mostly passed beyond into the lophodont and symborodont types, and the Artiodactyls were approximately in the stage of sub-types c; but the Lemuroidea, Creodonta, Insectivora, etc., were, almost without exception, tritubercular.

There can be little doubt that, parallel with the tritubercular forms, in each period, there were aberrant or degenerate types, but it is difficult to determine which these are. Many Mesozoic types, which the writer formerly considered aberrant, have now proven to be tritubercular.[3] The upper Jurassic genera included under the *Dicrocynodontidæ* (see Marsh, *Amer. Journ. Sc.*, April, 1887, p. 338) are apparently aberrant. There are several degenerate types among the Puerco and Wasatch Creodonts, such as *Dissacus* and *Mesonyx*. But there is a striking proof of the superiority of the tritubercular molar in the fact that, according to our present knowledge at least, the Jurassic mammals possessing aberrant or degenerate molar types did not persist into the Puerco, nor did such types in the Puerco persist into the Bridger. There is some doubt as to the persistence of the sub-tritubercular stage; the writer previously considered the *Thylacinus* molars as triconodont; but Mr. Lydekker has called attention to the probability that the metaconid has disappeared and been replaced by a heel as in the sectorial teeth of the Carnivora. The disappearance of the degenerate types may be attributed to the general principle that rapid specialization and loss of parts leads ultimately to extinction, by depriving the animal of the means of adaptation to new conditions, or surroundings.

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[3] See "Additional Observations upon the Structure and Classification of the Mesozoic Mammalia." Proc. Phila. Acad., Nov., 1888.

The mechanical superiority of the tritubercular type, over every other has been repeatedly demonstrated in its plastic capacity of adaptation to the most extreme trenchant and crushing functions.

THE ARTIODACTYLA.[1]

BY E. D. COPE.

THE Artiodactyla is the suborder of the Diplarthrous Ungulata in which the astragalus articulates with the second row of tarsal bones by a ginglymus or hinge, and in which the third and fourth toes are equally or subequally developed.[2] It includes the most highly modified of the Mammalia, whether we regard the organs of locomotion or of digestion. The antelope and deer illustrate the greatest speed to which the mammal has attained. Their extraordinary apparatus for the digestion of vegetable substances which contain but a small percentage of nutritious proteids, has given them an extraordinary advantage, so that they are after the rodents, the most abundant of their class, in spite of the persistent persecution of the carnivorous species. They attain in the genera Giraffa and Bos the largest dimensions in the class, excepting only the Proboscidia.

The Artiodactyla make their first appearance in the early or Wasatch Eocene in the genus Pantolestes Cope. A genus exists at a corresponding horizon in Europe. No other genus of the suborder appears with it. Its representatives steadily increase in numbers in the succeeding Bridger and Uinta epochs in America, and in the Calcaire grossier and Gypse of Europe. Some of these, *e.g.*, the Anoplotheriidæ of Europe, diverge from the line of succession, while others, *e.g.*, Xiphodontidæ, are clearly ancestors of later forms. In America, the Pantolestidæ appear as ancestors of the Camels especially. I now give a synopsis of the families of the suborder and their phylogenetic relations.

I. Superior molars tritubercular (Pantolestoïdea).

Molars bunodont; four digits............................... *Pantolestidæ.*

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[1] Modified for the Naturalist from a paper by the author in the Proceeds. of Amer. Philos. Society, 1887, p. 377.

[2] See Naturalist, November, 1877.